Density and Species Diversity of Bird Populations in *Eucalyptus* Forests in Victoria, Bass Strait Islands, and Tasmania

By Ian Abbott*

ABSTRACT: Bird populations in *Eucalyptus* forests on three islands in Bass Strait, Tasmania and Victoria were counted during 1969-1971. No difference in diversity between mainland and island bird populations was found. Diversity, and number, of land bird species were highly correlated. Population densities of birds were lower in the non-breeding season. Total population densities did not differ between island and mainland habitats studied. Average density per species in the breeding season on the islands was 13% less than on the mainland, but in the two cases studied in the non-breeding season was 40% higher. Island species were more equally abundant during the breeding season than mainland species.

In the breeding season, population densities of six species were higher on islands than on mainland, and for five species were lower on the islands. This is consistent with Janzen's demonstration that the arthropod faunas of islands are non-random samples of the mainland fauna, and with a hypothesis that island bird species which forage in places where the arthropod fauna is impoverished will be rarer than on the mainland, and conversely.

INTRODUCTION

Without exception, islands support fewer breeding species of birds than an equal-sized area of the nearest mainland. The probable explanation is that most species in a community are rare (Preston 1948, Williams 1964), so that on islands these tend to become easily extinct and are not quickly replaced because of isolation (MacArthur & Wilson 1967). Also, many species are absent because they cannot cross to the island often enough or in large enough numbers to effect establishment (Abbott 1972, 1973, 1974). Often the populations of species present on islands become even denser than they are on the mainland, owing to a relaxation in competition (Crowell 1962, Grant 1966 *a*, *b*) and predation (Grant 1966 *b*).

My study on the bird populations in *Eucalyptus* forests in Victoria, three islands in Bass Strait and Tasmania was designed to see whether such forests on islands also support an impoverished avifauna relative to mainland forests. The question is complex, because impoverishment may *a priori* mean that the number of species, the total number of individual birds (or their density), or the diversity of bird species (where diversity refers to the weighting of species number by population size) in *Eucalyptus* forests is lower on islands than mainland.

These three aspects of impoverishment interrelate, and all need consideration. Thus, because islands have fewer bird species than equal-sized mainland areas, interspecific competition should be relaxed, resulting in populations of some bird species increasing in density. This should result in *Eucalyptus* forests on the islands having a smaller diversity of bird species in comparison with *Eucalyptus* forests on mainland Victoria.

AREAS STUDIED, AND METHODS

Censuses of eight areas were made during 1969-71; five of these areas were on islands (Fig. 1). The mainland areas, being more accessible from Melbourne, were censused more frequently than those on the islands, most of which were censused only once. Details of sites are as follow.

Creswick. Five censuses of one plot, and four

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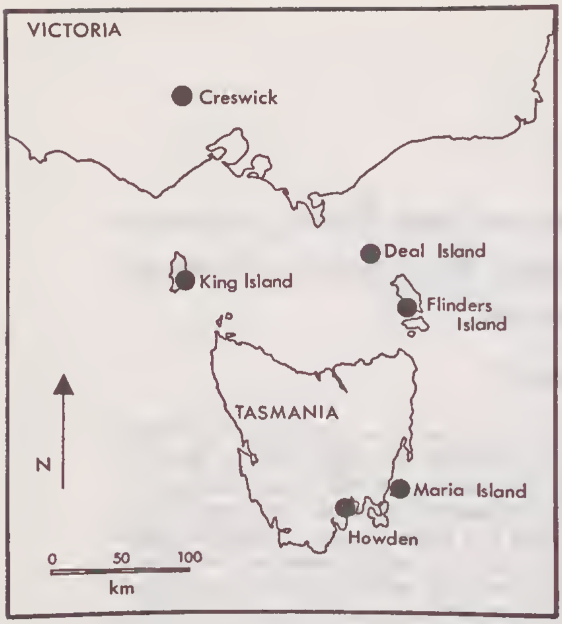

FIG. 1—Location of plots on which censuses of bird populations were made.

each of two other plots, were made. All plots consisted of *Eucalyptus dives* and *E. obliqua* dry sclerophyll forest with undergrowth of *Acacia* spp. Censuses of a plot adjacent to the Victorian Forestry School were made during August 1969 (1), October 1969 (6), November 1969 (7), May 1970 (2) and September 1970 (8). The numbers in parentheses refer to code numbers of each census in Appendix 1. Four censuses of the second plot (next to St. Georges Lake) were done, in October 1969 (9), November 1969 (10), May 1970 (3) and September 1970 (11). In August 1969 (4), October 1969 (12), November 1969 (13) and May 1970 (5), a census of the third mainland plot (at Leonards Hill) was made.

Deal Island. A census of this plot, in the gully between the lighthouse and living quarters, was made in March 1971 (2, Appendix 2). Vegetation was dominated by *Eucalyptus nitida* of mallee habit, with undergrowth of *Leptospermum, Acacia* and *Casuarina.*

Flinders Island. Censuses of this plot, on the south facing slope of Smiths Gully, were done in November 1969 (3), April 1970 (1) and November 1970 (4). (Numbers in parentheses refer to censuses in Appendix 2). The forest was composed of *Eucalyptus obliqua, E. globulus* and *E. viminalis,* with understorey of *Acacia, Melaleuca* and *Pteridium.*

King Island. One census of a plot on the south facing slope of Raffertys Gully in the Pegarah Forestry Reserve was made during October 1970 (5, Appendix 2). Vegetation was as for Flinders Island plot except that *Pteridium* was absent.

Maria Island. One census of a plot, NE. of the abandoned farm near Chinamans Bay, was done in November 1970 (6, Appendix 2). Vegetation in the plot consisted of *Eucalyptus globulus, E. obliqua* and *Acacia* sp.

Howden, Tasmania. A census of a plot, on the eastern side of Mt. Louis, was made in November 1970 (7, Appendix 2). Dominant trees were of *Eucalyptus tasmanica, E. linearis* and *Acacia* sp.

In choosing these plots, an effort was made to pick areas with trees of similar height and with similar proportions of vegetation and of open space. All plots were approximately 32,400 m^2 (8 acres) in area. (The figure of 10 acres was mistakenly used by Abbott 1973; the correct figure is however given in Abbott 1972.) All plots were representative of the extensive *Eucalyptus* habitats found in lowland Victoria, coastal Tasmania and the Bass Strait Islands.

In order to make the census of each plot as thorough as possible, I counted birds at dawn, early morning and late afternoon, usually on five consecutive days. Consequently this left no time for me to make censuses of other habitats on the islands. My aim was to make a census of one area as completely as possible, rather than of a number of plots superficially. All parts of a plot were covered many times during each census.

A grid of 33·3 m (100 ft) squares was marked over each plot. The position of birds sighted and heard, and their movements and nests, were noted on hand maps of the plot. Territorial boundaries and the number of sedentary individuals on the plots were thus determinable. My chief interest was the sedentary individuals, since these have to feed and find shelter in the plot. Criteria for an individual to be proved sedentary were that it must be consistently found in a similar part of the plot or, if not, have most of its home range within it. Individuals not meeting these conditions are treated as transients, and are marked + in Appendices 1 and 2. Some species in each plot were represented by resident individuals and transients. However, the number of these transient individuals is not recorded in the Appendices because it varied from hour to hour, and those present may or may not have been feeding. These techniques are justified relative to other popular techniques in detail in Abbott (1972, pp. 27-29).

RESULTS

The results of censuses are given in full in the Appendices. Autumn and Winter censuses are grouped as Non-breeding censuses, and Spring-

Summer ones as Breeding censuses. Diversity of bird species is measured as:

$$D = -\sum_{i=1}^{S} p_i \ln p_i$$

where p_i is the proportion of individuals in the i^{th} species (i = 1, . . ., S). Also listed in the Appendices are the average population density per species, the maximum possible diversity of bird species for each plot (ln S), and J, a measure of evenness of the abundance of species. As shown by Lloyd and Ghelardi (1964), D has two separable components, species richness (S) and equitability of abundances, J (= D/ ln$S$), where $0 \leqslant S \leqslant \infty$ and $0 \leqslant J \leqslant 1$.

D and ln S are highly correlated (Fig. 2), implying that diversity of bird species can be described by simply counting the number of species. This is surprising, because counting species and ignoring their abundances should give biased results in that rare species are overemphasized and common species underemphasized. This result also holds for censuses in North America (Tramer

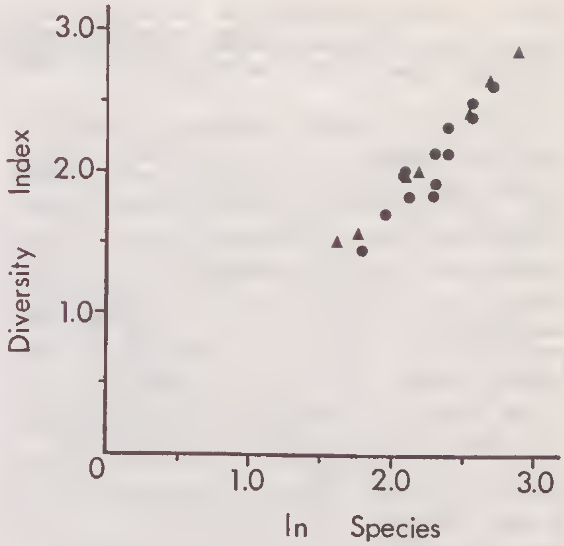

FIG. 2—Scatter diagram of relation between diversity of bird species and $\log_e$ number of species. Correlation coefficient = ·96, P < ·001. ● mainland censuses; ▲ island censuses.

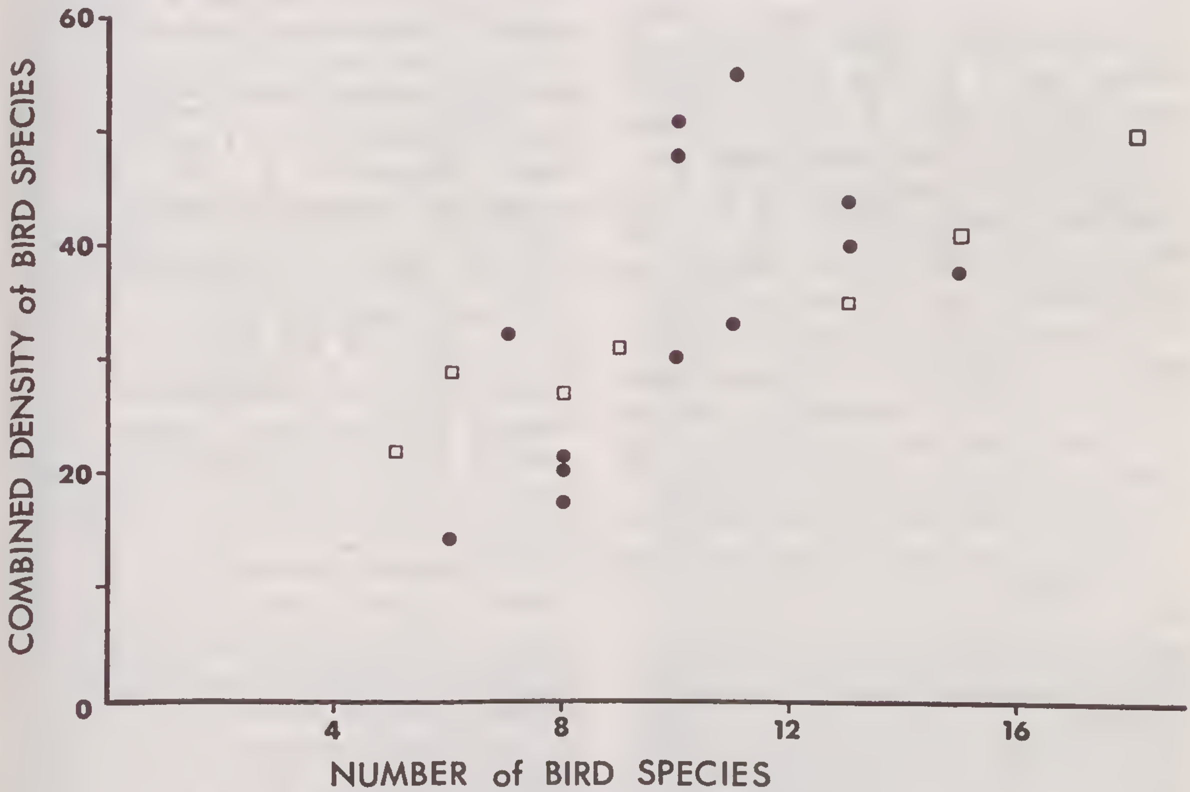

FIG. 3—Scatter diagram of relation between total density of all sedentary bird species and number of these species. Correlation coefficient = ·68, P <·01. ● mainland censuses; □ island censuses.

1969). Tramer concluded that the factors determining diversity of bird species really determine how many species can live together in a community.

My data for breeding censuses are adequate to look for differences in density, diversity, species richness and equitability between island and mainland plots. The total population density (= total number of sedentary individuals, because all areas are of same size) for mainland plots is slightly higher than for island plots, but the difference is non-significant (Table 1). As expected, total population densities are less during the non-breeding season. The average density per species in the breeding censuses is 13% lower on island plots than on mainland plots; in the non-breeding season, the two available island censuses have a 40% higher mean density per species than those of the mainland plots. Furthermore, the total population density of all sedentary bird species is highly correlated with the number of these present in each plot (Fig. 3). This therefore means that as the number of species packed into a habitat increases, the total density increases in a regular way.

The total population density can be further analysed by comparing densities in the island and mainland plots, as in Table 2. For statistical reasons, species sedentary in only one mainland or island plot are not considered. Out of 12 cases of censuses made in the breeding season, population densities of six species were higher on the island plots, population densities of five were higher on the mainland plots, and there was one species for which densities were unchanged. In the non-breeding season, data for only two cases are available: one shows an increase in population density on the island plots, the other a decrease. Thus the result above, that total population densities on the island and mainland plots are not significantly different, can be understood as being brought about by equal numbers of species on the island plots increasing or decreasing in density.

The island plots have more species of birds in the breeding season than do the mainland plots, but the difference is not significant (Table 1). Equality of species numbers in 8 acre plots on mainland and islands is to be expected from species-area curves (Preston 1962). In the breeding season, the diversity of bird species on islands is higher than on the mainland, but not significantly so (Table 1). The equitability component of diversity is significantly higher in the breeding season in island plots than mainland plots (Table 1), meaning that abundances are more evenly divided among the species present in the island plots.

DISCUSSION

If competition is the unremitting and pervasive process in nature that many ecologists believe (e.g. Lack 1971, MacArthur 1972), then these results should be easily explained in terms of competition theory. Because islands have fewer species of birds than equal-sized areas of mainland, many vacant niches should exist (Keast 1968, 1970), and in consequence the small number of species of birds present on islands should expand into these, and so change in distribution and abundance as compared with the mainland. The evidence for and against distributional changes on the Bass Strait islands and Tasmania has been discussed by Abbott (1973). On islands, the expected overall change in abundance of species present is that more species should be commoner than on the mainland. A change of this kind can be looked at in many ways. Total population density, average density per species, equitability and diversity should change in predictable directions on islands. None of these occurred with the bird communities in *Eucalyptus* forest in Tasmania and the islands of Bass Strait.

Diamond (1970) found that total population densities in coastal lowland rainforest on islands off New Guinea were 41-77% less than in the same habitat in New Guinea. Precisely the opposite condition is found on Bermuda (Crowell 1962), Tres Marías (Grant 1966*a*, *b*) and Islas Perlas (MacArthur et al. 1972). These last authors argue that decreased density of birds on islands would occur when few mainland species reach such islands, and the available habitats are occupied by less appropriate species. However it is difficult to decide independently which species are less appropriate than others. Bird species in *Eucalyptus* forests on the islands in Bass Strait and Tasmania are mostly the same as those in the mainland *Eucalyptus* forests studied. Species sedentary in my mainland plots but absent from the island plots are *Eopsaltria australis, Climacteris leucophaea, Meliphaga leucotis, M. chrysops,* and *Strepera versicolor*. The first three have similar ecological representatives in the island endemics *Petroica vittata, Melithreptus validirostris* and *Meliphaga flavicollis* respectively (pers. obs., Ridpath and Moreau 1966). Thus only two mainland species are in effect missing from the island habitats I censused.

Another possible explanation for altered densities of island birds is that the level of predation is different on islands relative to the mainland (Grant 1966 *b*). Most islands have few species of predators compared with the mainland number. On my island plots, up to six species of predatory

TABLE 1
POPULATION STATISTICS FOR MAINLAND AND ISLAND FOREST COMMUNITIES OF BIRDS.

Statistic	Mainland	Island	Significance (if tested with *t*-test)
Total population density			
Breeding season	38.1 ± 3.5	36.8 ± 4.0	NS
Non-breeding season	27.6 ± 7.5	25.5	-
Total no. species			
Breeding season	11.3 ± 0.8	12.6 ± 1.9	NS
Non-breeding season	8.0 ± 0.8	5.5	-
Diversity in avifauna			
Breeding season	2.22 ± 0.10	2.37 ± 0.17	NS
Non-breeding season	1.83 ± 0.12	1.53	-
Equitability			
Breeding season	0.92 ± 0.02	0.95 ± 0.07	$P < .001$
Non-breeding season	0.89 ± 0.11	0.90	-
Average density per species			
Breeding season	3.44	3.00	-
Non-breeding season	3.31	4.62	-

Note: NS means $P > .05$.

birds occur compared with four on the mainland plots. No overall quantitative comparisons are possible because most are transients. In addition, foxes occur on the mainland plots (but not island ones), and cats on some of the island and mainland plots. Snakes were seen only on some island plots. These facts are insufficient to prove or disprove the predation hypothesis.

If the arthropods on islands are a non-random selection of those available on the adjacent mainland (Janzen 1973), the species of birds that increase in density should be those whose food supply consists of those arthropod species that are well represented and common on the islands. Bird species that decrease in density (or even become extinct) should, on this hypothesis, be those whose food supply is poorly represented on islands. On this hypothesis, *Malurus cyaneus* and

TABLE 2
DENSITY OF 16 SPECIES OF BIRDS IN MAINLAND AND ISLAND *Eucalyptus* HABITATS

Species	Mean Density (No. Cases)	
	Mainland	Island
Breeding season		
Malurus cyaneus	5.0 (4)	2.7 (3)
Rhipidura fuliginosa	3.9 (8)	5.0 (3)
Petroica multicolor	2.2 (5)	3.3 (3)
Pachycephala pectoralis	2.0 (6)	2.7 (3)
P. olivacea	2.0 (2)	2.0 (2)
Colluricincla harmonica	2.3 (6)	2.0 (2)
Pardalotus punctatus	2.4 (5)	3.3 (3)
P. striatus	2.0 (2)	2.7 (3)
Meliphaga leucotus / M. flavicollis	13.0 (3)	4.6 (5)
Melithreptus lunatus / M. affinis	4.0 (4)	3.3 (3)
Eopsaltria australis / Petroica vittata	2.3 (6)	3.0 (4)
Sericornis frontalis / S. humilis	5.4 (7)	2.7 (3)
Non-breeding season		
Rhipidura fuliginosa	1.3 (3)	6.0 (2)
Sericornis frontalis / S. humilis	7.0 (4)	5.0 (2)

Source: Appendix.

Sericornis spp. are not so common on the island plots as the mainland plots (Table 2) because the arthropods they prefer or hunt for on the ground are scarce. *Rhipidura fuliginosa* would be commoner on the islands (Table 2) because the arthropods it hunts for (insects taken in mid-air) are common. This is an attractive general hypothesis that would account for the differences between the North American and Australian/New Guinea islands in bird densities. More critical data need to be collected so that this hypothesis, the predation hypothesis and the competitive release hypothesis may be tested.

CONCLUSIONS

1. Eight acre areas of *Eucalyptus* forests on three Bass Strait islands and Tasmania have (a) approximately the same population density of

bird species, (b) similar numbers of bird species, and (c) approximately the same diversity of bird species as such areas on mainland Victoria.

2. Of 12 bird species found on more than one island and one mainland plot, six had higher densities on the islands, five had the reverse and one was unchanged in density.

3. The hypothesis that competition between bird species is relaxed on these islands is not supported. Differences in the level of predation, and intrinsic differences in the food supply, between *Eucalyptus* forests on the islands and the mainland may be responsible for changes in population density of bird species.

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APPENDIX 1. CENSUSES OF MAINLAND PLOTS

1-5 Non-breeding season; 6-13 Breeding season

Species	1	2	3	4	5	6	7	8	9	10	11	12	13
Glossopsitta concinna												+	
Platycercus elegans	+	+	+	+	+	+	+	+	+	+	+	+	+
Cacomantis pyrrhophanus											+	2	2
Chrysococcyx sp.								2+	1		+		
Dacelo novaeguinae			+			+		+					
Coracina novaehollandiae												+	
Turdus merula	+	+	2+			+	+	+		4	4		
Zoothera dauma	2												
Cinclosoma punctatum				2									
Acanthiza pusilla	4+	+	+	2+	+	5+	6+	2+	6+	2+	2+	1	
A. chrysorrhoa	+	+				3+	4+	+			+		
A. striata								+			+		
A. reguloides	+					+		+					
Sericornis frontalis	2	+	8+	8	10+	4	2+	+	2	6+	4+	10	10+
Malurus cyaneus	+	+	+	8	6+	+	4+			6	+	4	6+
Ripidura fuliginosa	1	2+	1		+	2+	2	5+	7	8	4	2	1
R. rufifrons							+						
Myiagra rubecula										+			
Petroica multicolor	2	4	2			2	3	2		2	2		+
P. rosea			+										
P. phoenicea		+	+										
Eopsaltria australis	2	1	2	2	2	2	2+	3		2	3	2	
Pachycephala rufiventris						4	4+	+					+
P. pectoralis	2	3+	2+		+	2	2	2	2	2	2		
P. olivacea				4+	2							2	2+
Colluricincla harmonica	+	+	+	4	+	2+	2	+	2	2	+	4	2
Climacteris leucophaea	2	2	2+	+	+	2+	4	3	2	2	2	+	
Pardalotus punctatus	+			4	+	2+	+	+	2	2+		4	2
P. striatus						2		+		2			
Zosterops lateralis	+	+	+										

APPENDIX 1 *(cont.)*

Species	1	2	3	4	5	6	7	8	9	10	11	12	13
Meliphaga chrysops	+	2				2	2	+	2+	+	5+		
M. leucotis		+	1	16+	8						1	20	18
Melithreptus lunatus			+	+	+		+		4	4+	4+	+	4+
M. brevirostris					+								
Phylidonyris pyrrhoptera				+	2+								
Acanthorhynchus tenuirostris		+		3	2+			+			+		
Anthochaera carunculata	+					2							
Aegintha temporalis	+							+					
Strepera versicolor	+	+		2		2	3	2				+	1
Corvus sp.	+		+			+		+					+
No. sedentary individuals	17	14	20	55	32	38	40	21	30	44	33	51	48
No. species	8	6	8	11	7	15	13	8	10	13	11	10	10
Diversity index	2.02	1.45	1.82	2.13	1.72	2.65	2.49	2.02	2.13	2.40	2.31	1.91	1.84
Average population density/species	2.13	2.33	2.50	5.00	4.57	2.53	3.08	2.63	3.00	3.38	3.00	5.10	4.80
ln no. species	2.08	1.79	2.08	2.40	1.95	2.71	2.57	2.08	2.30	2.57	2.40	2.30	2.30
J	.97	.88	.89	.88	.87	.98	.97	.97	.93	.93	.96	.83	.80

Note: + indicates transient individuals (See text).

APPENDIX 2. CENSUSES OF ISLAND PLOTS

1-2 Non-breeding season; 3-7 Breeding season

Species	1	2	3	4	5	6	7
Accipiter sp.	+						
Falco berigora				2			
Coturnix ypsilophorus						2+	
Turnix varia				+			
Phaps elegans					+		
Calyptorhynchus funereus			+		+	+	
Lathamus discolor						2+	
Platycercus eximius							+
P. caledonicus	+	+	+	+	+	+	
Cuculus pallidus			2	2		+	
Cacomantis pyrrhophanus			3+	+	+	+	
Chrysococcyx sp.				+			

Appendix 2 *(cont.)*

Species	1	2	3	4	5	6	7
Ninox novaeseelandiae					+		
Dacelo novaeguinae			2	+		+	
Petrochelidon nigricans						4+	+
Coracina novaehollandiae					+	+	2
Turdus merula	+	2+		+		+	+
Acanthiza pusilla		6+					
A. ewingi	+		+	+	2+		
A. chrysorrhoa						+	
Sericornis frontalis/humilis	2+	8+	4+	2+	2+		
Malurus cyaneus	4+		4+	2	2+		
Rhipidura fuliginosa	10+	2+	4+	5	6+	+	
Myiagra cyanoleuca		+		+		2	
Petroica multicolor	+		4	4		2	+
P. phoenicea	+	+	2	1		+	
P. vittata	+		4	3	+	2	3
Pachycephala pectoralis	2	+	2	4	2+	+	
P. olivacea	+		2	2		+	
Colluricincla harmonica	+		2	2+	+		+
Pardalotus punctatus	+		4	2+		+	4
P. striatus	2+		2	4+		2	+
P. quadragintus				2		+	6+
Zosterops lateralis	+	+		+	+	+	
Meliphaga flavicollis	9		3+	4+	8	2	6
Melithreptis lunatus		+					
M. affinis	+		2+	+	+	4+	2+
M. validirostris	+		+	+	3+	+	+
Phylidonyris pyrrhoptera	+	4		+	5+	+	
P. novaehollandiae					+	8+	+
Acanthorhynchus tenuirostris	+					2+	
Anthochaera paradoxa						2	2
Emblema bella						1	
Sturnus vulgaris	+		2+	+	+	+	
Artamus cyanopterus							2
Corvus sp.	+		2+			+	+
No. sedentary individuals	29	22	50	41	31	35	27
No. species	6	5	18	15	9	13	8
Diversity index	1.56	1.50	2.84	2.63	2.01	2.41	1.98
Average population density/species	4.83	4.40	2.78	2.73	3.44	2.69	3.38
ln no. species	1.79	1.61	2.89	2.71	2.20	2.57	2.08
J	.87	.93	.98	.97	.91	.94	.95

Note: + indicates transient individuals (See text).